

# Soil mesofauna may buffer the negative effects of drought on alien plant invasion

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## Abstract

1. Although many studies have tested the direct effects of drought on alien plant invasion, less is known about whether drought affects alien plant invasion indirectly via interactions of plants with other groups of organisms such as soil mesofauna.
2. To test for such indirect effects, we grew single plants of nine naturalized alien target species in pot mesocosms with a community of five native grassland species under four combinations of two drought (well-watered vs. drought) and two soil-mesofauna inoculation (with vs. without) treatments.
3. We found that drought decreased the absolute and the relative biomass production of the alien plants, and thus reduced their competitive strength in the native community. Drought also decreased the abundance of soil mesofauna, particularly soil mites, but did not affect the abundance and richness of soil herbivores. Soil-fauna inoculation did not affect the biomass of the alien plants but increased the biomass of the native plant community, and thereby decreased the relative biomass production of the alien plants. This increased invasion resistance due to soil fauna, however, tended ( $p = 0.09$ ) to be stronger for plants growing under well-watered conditions than under drought.
4. *Synthesis.* Our multispecies experiment thus shows that soil fauna might help native communities to resist alien plant invasions, but that this effect might be weakened under drought. In other words, soil mesofauna may buffer the negative effects of drought on alien plant invasions.

## KEYWORDS

alien-native competition, biological invasion, climate change, exotic, plant–environment interactions, soil animals

## 1 | INTRODUCTION

With the rapid globalization, more and more plant species have been introduced to new regions outside their native range (Seebens

et al., 2018; van Kleunen et al., 2015, 2018). Some of these alien plants have become invasive, which could decrease native species diversity and change nutrient cycles, thereby affecting the ecosystem functions (Hejda et al., 2009; Linders et al., 2019; Pyšek et al., 2012, 2020; Vilà et al., 2011). Forecasts show that the number

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of alien plant species per continent may increase on average by 18% from 2005 to 2050 (Seebens et al., 2021), indicating that the impacts of plant invasions on ecosystems may become even more severe. However, as there are many potential drivers of invasions, there are many uncertainties about how invasions and their impacts will develop in the future (Essl et al., 2020). In this regard, particularly the potential effects of ongoing global environmental change on plant invasions have garnered interest (Bartz & Kowarik, 2019; Liu et al., 2017, 2022; Speißer et al., 2021; Wang et al., 2022).

Nutrients and water are key resources for plant growth, and changes in their availabilities are important components of global change that may influence the invasion by alien plants (Bradley et al., 2010; Davis et al., 2000; Dukes & Mooney, 1999; Liu et al., 2017). Yet, evidence for the effect of changes in water availability, and particularly of drought, on alien plant invasion is not as clear-cut as those of nutrient availability. For example, a global empirical study on 64 grasslands (Seabloom et al., 2015) and a meta-analysis (Liu et al., 2017) provided evidence that nutrient enrichment promotes the performance of successful alien plants more strongly than the performance of natives. On the other hand, the limited number of case studies testing the effects of drought on alien plant invasion showed mixed results. For example, Manea et al. (2016) found that drought reduced the biomass production of native grasses, and consequently promoted the establishment success of alien plants. Similarly, Mojzes et al. (2020) showed that drought increased the performance of the invasive *Conyza canadensis* by decreasing the abundance, and thus competitive effect, of native grasses. However, other studies found that some invasive plants may suffer more from drought than native species, indicating that drought could also suppress alien plant invasion (Copeland et al., 2016; Kelso et al., 2020; LaForgia et al., 2018; Liu et al., 2017; Valliere et al., 2019; Werner et al., 2010). One of the reasons for the mixed findings could be that most studies did not consider interactions of the plants with other organisms (Copeland et al., 2016; Liu et al., 2017; Pintó-Marijuan et al., 2017; Valliere et al., 2019). Recent studies found evidence that other trophic levels could indirectly mediate the responses of alien plants to nutrient availability and variation therein (Li et al., 2022; Zhang et al., 2021). However, whether drought can affect alien plant invasion via other trophic levels remains largely unknown.

Soil mesofauna includes several important below-ground trophic groups that are increasingly recognized to affect plant competition (Endlweber & Scheu, 2006, 2007). Some of them could enhance nutrient mineralization, thereby increasing the plant nutrient uptake. For example, Bardgett and Chan (1999) showed that Collembola (i.e. mesofauna) increased nitrogen mineralization and nutrient leaching in grassland soils, and shoot nitrogen content of the grass *Nardus stricta*. Given that invasive plants frequently respond more positively to nutrient enrichment than native plants (Liu et al., 2017, 2018), such soil mesofauna may increase the invasion success of alien species by increasing soil nutrient availability. On the other hand, soil fauna can also change alien-native competition via detrimental impacts on plants (Korell et al., 2019). The enemy-release hypothesis poses that alien plants are released from most of their specialist natural

enemies (Keane & Crawley, 2002; Liu & Stiling, 2006; Mitchell & Power, 2003; Vilà et al., 2005). Following this logic, alien plants should be damaged less than natives by root herbivores, such as some Collembola taxa belonging to the families Onychiuridae and Sminthiridae (Chahartaghi et al., 2005; Endlweber et al., 2009). Consequently, if the soil-mesofauna communities include such plant enemies, the presence of soil mesofauna should promote alien plant invasion due to the enemy release of alien plants. However, until now very few studies have tested whether, and if so how, the presence of soil mesofauna affects alien plant invasion into native communities.

It has been found that indirect effects of altered biotic interactions due to climate change on animal populations are more pronounced than their direct effects (Ockendon et al., 2014), which may also be the case for plant populations. For example, empirical studies indicated that below-ground trophic interactions could alter plant responses to drought (Erb et al., 2011; Franco et al., 2020; Guyer et al., 2018; Wilschut & van Kleunen, 2021). Consequently, it is likely that drought might indirectly affect alien plant invasion into resident communities via effects on soil organisms. Indeed, drought can reduce the abundance and diversity of soil fauna (Aupic-Samain et al., 2021; Eisenhauer et al., 2012; Guyer et al., 2018; Makkonen et al., 2011; Wilschut & Geisen, 2021). Given that soil fauna, and in particular some of the root herbivores, might suppress native plants more strongly than they suppress alien plants (Korell et al., 2019), the reduction in soil fauna caused by drought might result in a higher apparent drought tolerance of native plants than of alien plants. However, whether this is the case has not been tested yet.

To test the effects of drought, soil mesofauna and their interaction on alien plant invasion into a native resident community, we performed a mesocosm-pot experiment. We grew single plants of nine alien target species in a community of five native grassland species under four combinations of two drought (well-watered vs. drought) and two soil-mesofauna inoculation (with vs. without) treatments. By comparing the absolute above-ground biomass production of the alien target species as well as their biomass production relative to the biomass production of the native competitors, we addressed the following specific questions: (1) Does drought suppress the absolute and proportional biomass of alien species in the native communities? (2) Does the presence of soil mesofauna promote or suppress the absolute and proportional biomass of alien species? (3) Does the presence of soil mesofauna change the effect of drought on the absolute and proportional biomass of alien species?

## 2 | MATERIALS AND METHODS

### 2.1 | Study species

To test the effects of drought, the presence of soil mesofauna and their interaction on alien plant invasion in a native grassland community, we chose nine naturalized alien species as targets and five native species as competitors (i.e. community members) from the herbaceous flora of China (see Table S1). We classified the species as

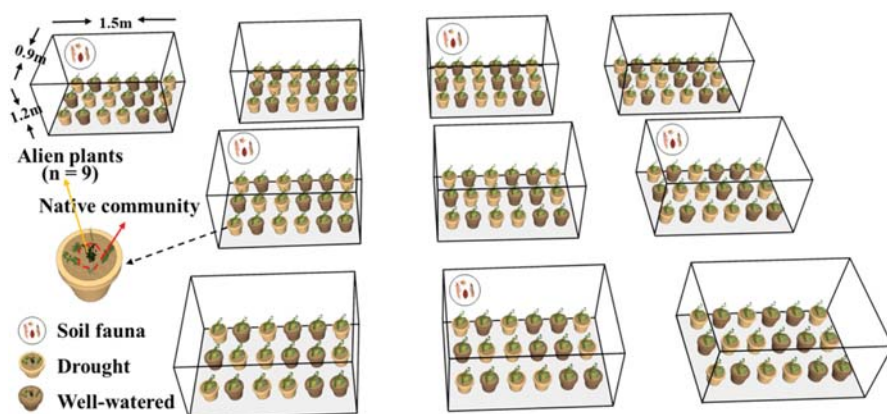


FIGURE 1 Graphical illustration of the experimental design.

naturalized alien or native to China based on information in the book 'The Checklist of The Naturalized Plants in China' (Yan et al., 2019) and the Flora of China database ([www.efloras.org](http://www.efloras.org)). To cover a wide taxonomic breadth, the nine alien species were chosen from eight genera of four families. The five native species, used to create the native community, included two forbs and three grasses that are all very common and do co-occur in many grasslands of China. Seeds of all species, except one, whose seeds were bought from a commercial seed company, were collected from natural populations growing in grasslands (Table S1).

## 2.2 | Soil-mesofauna collection

To provide a live soil-fauna community as inoculum for the pot mesocosms, we collected soil mesofauna from a grassland site, where the five species used to create the native resident communities also occur, at the Northeast Institute of Geography and Agricultural Ecology, Chinese Academy of Sciences (125°24'03"E, 43°59'49"N). On 21 July 2020, we removed above-ground plant materials from each of the 100 sampling locations (30 cm × 30 cm), and then collected from each location a soil sample of 1 L (10 cm × 10 cm × 10 cm) using a shovel. Each sampling location was at least 10 m apart from the others. Then, we brought the 100 soil samples to the laboratory, where we extracted the soil mesofauna communities of each soil sample separately using Berlese-Tullgren extractors without heating (Tullgren, 1918). In brief, we put each soil sample separately on top of a stainless steel soil-sieve with a 2-mm mesh size, and then waited 12 days so that many of the soil organisms would fall through the holes, via stainless steel funnels, into plastic bottles filled with 50 ml of soil-fauna-free peat moss (Pindstrup Plus, Pindstrup Mosebrug A/S, Denmark). On 2 August 2020, we finished the soil-mesofauna community collection. We then randomly chose 10 of the 100 soil-mesofauna communities for soil-fauna investigation (see Table S2), and used the remaining 90 soil-mesofauna communities for inoculation of the soil in the 90 experimental pot mesocosms (i.e. one soil-mesofauna community per mesocosm). We did not find any microfauna such as nematodes in the soil-fauna communities, indicating that this

study indeed only tested the effects of mesofauna communities on alien plant invasion in response to drought.

## 2.3 | Experimental set-up

To compare the growth performance of alien plants when growing in a resident native grassland community under different drought and soil-mesofauna inoculation treatments, we did a mesocosm-pot experiment in a greenhouse of the Northeast Institute of Geography and Agricultural Ecology, Chinese Academy of Sciences. We grew each of the nine alien species in the centre of a matrix of the native community under two water availabilities (well-watered vs. drought) and two soil-mesofauna inoculation (with vs. without) treatments. For each of the nine alien species, we had five replicates for each of the four drought × soil-fauna inoculation treatment combinations, resulting in a total of 180 pots (9 alien species × 2 soil-mesofauna inoculations [with vs. without] × 2 drought treatments [well-watered vs. drought] × 5 replicates).

From 15 May to 5 July 2020, we sowed the seeds of each species separately into plastic trays (195 mm × 146 mm × 65 mm) filled with peat moss as substrate (Pindstrup Plus, Pindstrup Mosebrug A/S, Denmark). As previous experiments have shown that the time required for germination differs among the species, we sowed the species on different dates (Table S1) to obtain similarly sized seedlings at the start of the experiment. On 3 August 2020, we filled 180 2.5-L circular plastic pots (top diameter: 18.5 cm, bottom diameter: 12.5 cm, height: 15 cm, Yancheng Tenge Plastics Co., Ltd, China) with the same substrate as used for germination. A possible side effect of drought treatment could be that it reduces nutrient availability by immobilizing the nutrients. Therefore, to reduce potential nutrient limitation as much as possible, we mixed 5 g of slow-release fertilizer (Osmocote® Exact Standard; Everris International B.V.) into the substrate of each pot. To create the native community, we selected similarly sized seedlings from each of the five native species, and transplanted one seedling of each native species at equal distances in a circle (diameter = 11 cm) around the centre of each pot. We then planted into the centre of each pot one seedling of one of the alien species. For each of the nine alien species, we had 20 pots.

After transplanting (i.e. on 3 August 2020), we randomly assigned two pots of each alien species to each of 10 plastic cages (150 cm × 90 cm × 100 cm; Figure 1). The 10 cages were covered with nylon nets (mesh size: 0.15 mm × 0.15 mm) to prevent soil mesofauna from entering or leaving the cages. We put a plastic dish under each pot, and regularly watered the pots before starting the drought treatment to ensure that none of the plants were water limited. We inoculated each pot in 5 of the 10 cages (i.e. 90 pots), each with 50 ml of one of the 90 soil-mesofauna inocula we had collected. As the soil-mesofauna inoculum also introduced another 50 ml of peat moss into the pots, we also added, as a control, 50 ml of the same peat moss (free of soil fauna) to each pot in the remaining five cages. We assigned the cages with and without soil-mesofauna inoculations to alternating positions that were at least 0.5 m apart from each other (Figure 1).

As we used the Berlese-Tullgren extractors to collect the soil fauna, we cannot exclude the possibility that soil microbes were also introduced with the soil animals. Therefore, we also used amplicon DNA sequencing of the peat moss with and without soil-fauna soil ( $n = 5$ ) to assess whether the diversity and composition of the soil microbes differed between them. Although the composition of the fungal community differed slightly between the two soil-fauna treatments, the richness and Shannon diversity of the bacterial and fungal communities did not differ (Figure S1), indicating that the soil-fauna inoculation treatment had minimal side effects.

On 14 August 2020 (i.e. 11 days after the start of the experiment), we started the drought treatment. One of the two pots of each alien target species in each cage served as a control (i.e. well-watered), while the other pot was exposed to the drought treatment. For the well-watered treatment, we watered all plants by filling the dish under each pot as soon as the substrate had absorbed the water from it. This way, the substrate stayed permanently moist and none of the plants lost leaf turgor throughout the entire experiment. For the drought treatment, we daily checked all pots, and when all plants of the community in a pot had wilted (i.e. had lost leaf turgor), we supplied the pot with 50 ml of water. The mean interval between two water-supply points of the drought treatment was 4 days (median = 3, range = 1–18).

On 28 September 2020, 52 days after the start of the drought treatments, we harvested the experiment. For each pot, we separately harvested the above-ground biomass of the alien target species and of the native community. As the roots of the plants were strongly intertwined, we could not harvest the below-ground biomass. All above-ground biomass was dried for at least 72 h at 65°C, and then weighed. Based on the above-ground biomass of the alien and native species, we calculated the biomass proportion of the alien target species (the biomass of the alien target species/[biomass of the alien target species + biomass of the native community]) as a proxy of the dominance of the alien target species (Liu et al., 2018; Parepa et al., 2013).

To test the effect of the drought treatment on soil fauna (in the pots that had been inoculated with soil fauna), we investigated the soil fauna of drought and well-watered pots after plant harvest. We first randomly selected one pot of each target alien species under drought or well-watered conditions, and then brought all soil of these pots

back to the laboratory. In total, we had 18 soil samples for soil-fauna extraction (9 alien species × 2 drought treatments [well-watered vs. drought] × 1 replicate). Using the Berlese-Tullgren extractors without heating, we extracted the soil-fauna communities of each soil sample separately, and obtained the total soil-fauna abundance, soil-mites abundance, soil-herbivore abundance and soil-herbivore richness for each sample. As most soil-fauna species in our samples were mites (c. 70.0%), and it was difficult to identify all of them to the species level, we do not have data of soil-fauna richness. It should also be noted that the soil herbivores were only identified to the order level and not to the species level, and thus the taxonomic richness may have been underestimated for each sample. We also did soil-fauna investigation for five pots that were randomly selected from the pots without soil-mesofauna inoculation, and found no soil fauna in these pots, indicating that our soil-mesofauna inoculation treatment and the isolation imposed by the cages were effective.

## 2.4 | Statistical analysis

All statistical analyses were conducted in R 4.0.3 (R Core Team, 2020). To analyse the effects of the drought and soil-mesofauna inoculation treatments, and their interaction on performance of the alien plants in the native community, we fitted linear mixed-effects models using the `lme` function of the `'nlme'` package (Pinheiro et al., 2020). Above-ground biomass production of the alien target species, the native community species and biomass proportion of the alien target species in each pot (i.e. target above-ground biomass/total above-ground biomass) were the response variables. To meet the assumption of normality, biomass production of the alien target species and the native competitor species were natural-log-transformed, and biomass proportion of the target species was logit-transformed. We included drought treatment (i.e. well-watered vs. drought), soil-mesofauna inoculation treatment (i.e. with vs. without) and their interaction as fixed effects in all models.

To account for non-independence of individuals of the same alien plant species and for phylogenetic non-independence of the species, we included identity of the target species and its corresponding family as random factors in all models. In addition to account for non-independence of plants within the same cage, we also included cage identity as a random factor in all models. As the homoscedasticity assumption was violated in all models, we also included variance structures to model different variances per species or per cage (based on model selection) using the `'varIdent'` function in the R package `'nlme'` (Pinheiro et al., 2020). We used log-likelihood ratio tests to assess significance of the fixed effects drought treatment, soil-fauna inoculation treatment and their interaction (Zuur et al., 2009). These tests were based on comparisons of maximum-likelihood models with and without the terms of interest, and the variance components were estimated using the restricted maximum-likelihood method of the full model (Zuur et al., 2009).

To determine in more detail how soil fauna, drought and their interaction affect biomass production of the alien and native species,

and the resulting biomass proportion of the alien target species, we built a structural equation model using the `psem` function of the 'PIECEWISESEM' package (Lefcheck, 2016). The effects of soil fauna, drought and their interaction on biomass production of native and alien species, as well as on alien proportion were modelled via linear mixed effects models using the `lmer` function of the 'LME4' package (Bates et al., 2015). The conceptual construct model is shown in Figure S2. In all linear mixed-effects models, the identity of the target species and cage identity were included as random factors. To yield single standardized coefficients representing the expected changes in endogenous variables (response variables) with changes in exogenous variables (predictor variables), we converted the categorical variables to binary variables (i.e. drought treatment: well-watered = 0, drought = 1; soil-mesofauna inoculation: without = 0, with = 1).

To test the effect of drought on total soil-fauna abundance, soil-mites abundance, soil-herbivore abundance and soil-herbivore richness, we applied Mann-Whitney *U* tests using the `wilcox.test` function of the 'STATS' package (R Core Team, 2020).

### 3 | RESULTS

Most of the nine alien target species, with the exception of *Bidens pilosa*, *Hibiscus trionum* and *Xanthium strumarium*, showed similar responses to the drought and soil-mesofauna inoculation treatments (Figure S3). Averaged across the nine alien target species, drought significantly decreased the above-ground biomass production of alien target species (−58.6%; Table 1; Figure 2a) and of the native community (−51.5%; Table 1, Figure 2b). As biomass of the aliens decreased more strongly in response to drought than biomass of the natives, the biomass proportion of the alien target species in each

pot decreased (−11.6%; Table 1; Figure 2c). Inoculation with soil fauna had no significant effect on above-ground biomass of the alien target plants, but had a significant positive effect on above-ground biomass of the native community (+40.1%; Table 1; Figure 2b). Consequently, the above-ground biomass proportion of the alien target species was decreased in the presence of soil fauna (−41.9%; Table 1; Figure 2c). Moreover, the native community was suppressed slightly less by drought in the absence of soil fauna (−49.1%) than in its presence (−53.2%; Table 1; Figure 2b). As this was not the case for the alien target species, the biomass proportion of the alien target species in response to drought tended to be negative (−20.9%) under conditions without soil fauna, whereas it tended to be positive under conditions with soil fauna (+6.9%; marginally significant *S*×*D* interaction in Table 1, *p* = 0.09; Figure 2c).

The structural equation model showed that drought had negative effects on above-ground biomass of both the alien target species and the native community (Figure 3). Drought had no direct effect on biomass proportion of the alien species, but it had indirect effects via aboveground biomass of the alien targets (joint coefficient: −0.3147; Figure 3) and native community (joint coefficient: 0.1962; Figure 3). It had an overall negative effects on biomass proportion of the alien species (joint coefficient: −0.1184; Figure 3). Soil-mesofauna inoculation had opposing direct effects on the alien target species and native community. Whereas it had a negative effect on above-ground biomass of the alien target species, it had a positive effect on above-ground biomass of the native community (Figure 3). Soil-mesofauna inoculation had no direct effect on proportional biomass of the alien target species, but it had indirect effects via above-ground biomass of the alien targets (joint coefficient: −0.1865; Figure 3) and native community (joint coefficient: −0.1667; Figure 3). It had an overall negative effect on biomass proportion of the alien species that was ~3 times stronger than the

**TABLE 1** Results of linear mixed-effects models testing the effects of drought (well-watered vs. drought), soil fauna (with vs. without) and their interactions on above-ground biomass production of the alien target plants, native competitor species and biomass proportion of the alien target species in each pot. Significant effects (*p* < 0.05) are in bold, and marginal significant effects (0.05 < *p* < 0.1) are underlined.

Fixed effects	Above-ground biomass production of the alien target species (natural-log-transformed)			Above-ground biomass production of the native competitor species (natural-log-transformed)			Above-ground biomass proportion of the target species in each pot (logit-transformed)		
	df	$\chi^2$	<i>p</i>	df	$\chi^2$	<i>p</i>	df	$\chi^2$	<i>p</i>
Soil fauna (S)	1	2.4990	0.1139	1	4.7722	<b>0.0289</b>	1	7.0803	<b>0.0078</b>
Drought (D)	1	63.8413	<b>&lt;0.0001</b>	1	164.1043	<b>&lt;0.0001</b>	1	5.6339	<b>0.0176</b>
S×D	1	0.1512	0.6974	1	5.6304	<b>0.0177</b>	1	2.8297	<u>0.0925</u>
Random effects	SD			SD			SD		
Family	0.004			0.002			0.004		
Species	0.970 <sup>a</sup>			0.086			1.057 <sup>a</sup>		
Cage	0.004			0.267 <sup>a</sup>			0.187		
Residual	0.586			0.126			0.555		
	Marginal <i>R</i> <sup>2</sup>		Conditional <i>R</i> <sup>2</sup>	Marginal <i>R</i> <sup>2</sup>		Conditional <i>R</i> <sup>2</sup>	Marginal <i>R</i> <sup>2</sup>		Conditional <i>R</i> <sup>2</sup>
<i>R</i> <sup>2</sup> of the model	0.138		0.770	0.641		0.940	0.063		0.802

<sup>a</sup>Standard deviations for individual alien species or individual cage random effects for the saturated model are found in Table S3.



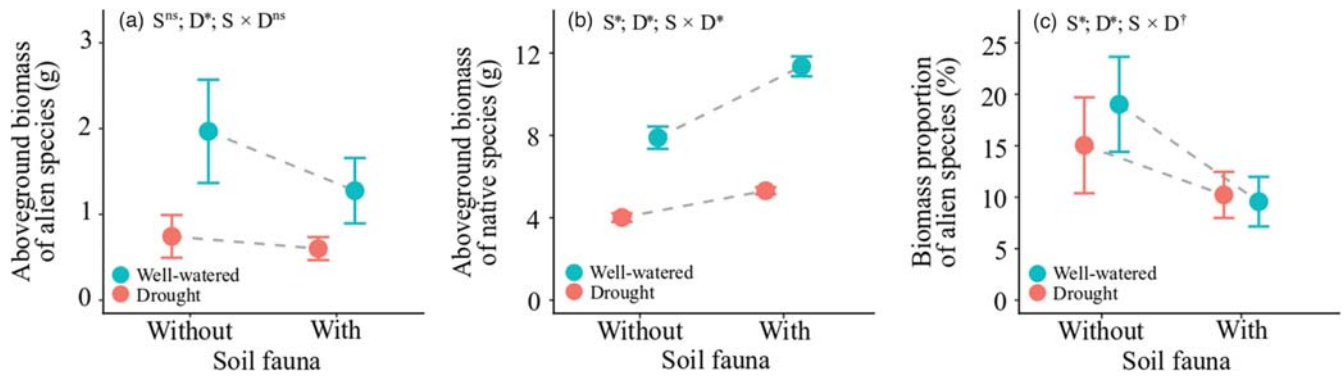


FIGURE 2 Mean values ( $\pm$  SE) of above-ground biomass of the alien target species (a), above-ground biomass production of the native competitor species (b) and biomass proportion of the alien target species in each pot (c) under different drought (well-watered vs. drought) and soil-mesofauna inoculation (with vs. without) treatments. Significant parameters (i.e. 'S' [soil fauna], 'D' [drought] and 'S × D') are indicted with asterisks (\*), the marginal significant ones are indicated with daggers (†), and the non-significant ones are indicated with 'ns'.

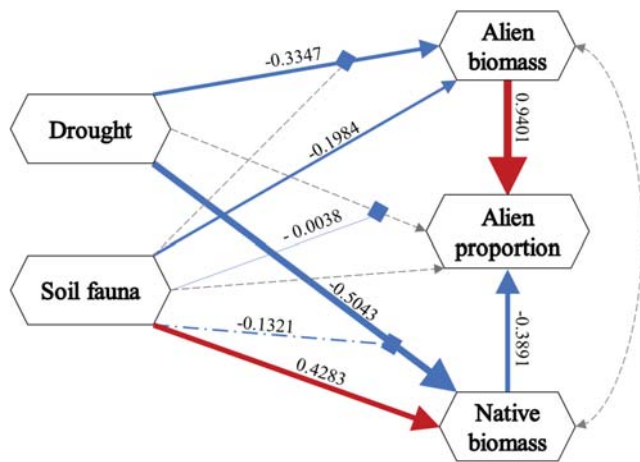


FIGURE 3 Structural equation model (SEM) showing the effects of drought, soil fauna and their interaction on biomass production of alien target species and native communities, as well as on biomass proportion of alien target species in the community. In the diagram, arrows indicate paths, and lines that connect to the paths at the squares (■) indicate interactions; solid arrows indicate significant paths ( $p < 0.05$ ); the dash-dotted line indicates a marginally significant interaction ( $0.05 < p < 0.1$ ); and the dashed arrows indicate non-significant paths ( $p > 0.1$ ). Positive paths are shown in red, negative paths are shown in blue. Numbers along the paths are standardized coefficients. For the model, Fisher's  $C = 0$  and  $p = 1$ , indicating there were no missing paths in the model.

effect of drought (joint coefficient:  $-0.3532$ ; Figure 3). The interaction between drought and soil-mesofauna inoculation on biomass of the alien target plants was not significant, but it was marginally significant for biomass of the native community. The presence of soil fauna made the negative effect of drought on the native community more intense. Consequently, the presence of soil fauna reduced the negative effect of drought on biomass proportion of the alien species by 43% (joint coefficient:  $-0.0670$ ; Figure 3).

Analysis of soil fauna, at the end of the experiment, for a subset of pots from the soil-mesofauna inoculation treatment showed that drought significantly decreased the total abundance of soil fauna

( $-57.4\%$ ; Figure 4a) and soil mites ( $-54.6\%$ ; Figure 4b), but did not affect soil-herbivore abundance and richness (Figure 4c,d).

## 4 | DISCUSSION

Our multispecies experiment found that drought limited the absolute and the proportional biomass production of the alien target plants. This means that drought suppressed the growth performance and thus reduced the competitive ability of the alien species in the native community. In addition, we found that the presence of soil-mesofauna communities benefited the native community and resulted in a decreased biomass proportion of the alien species. In other words, the presence of soil fauna promoted the resistance of the native community against invasion by alien species. Moreover, the suppressive effect of drought on biomass proportion of the alien plants tended to disappear (although this effect was only marginally significant;  $p = 0.09$ ) in the presence of soil fauna. In line with this, the structural equation model also showed that the presence of soil fauna negated the negative effect of drought on alien plant invasion into the native community (i.e. dominance of the alien plant decreased by 43%).

While drought is well known to reduce plant performance overall (Beierkuhnlein et al., 2011; Gupta et al., 2020; Zlatev & Lidon, 2012), recent studies found that growth and reproduction were more strongly affected for invasive than for native plant species (Kelso et al., 2020; Liu et al., 2017; Valliere et al., 2019). Our results are consistent with these previous findings (see also the total biomass production per pot in Figure S4), and suggest that the native competitors were more tolerant to drought than the invasive alien species (Copeland et al., 2016; Kelso et al., 2020; LaForgia et al., 2018; Liu et al., 2017; Valliere et al., 2019; Werner et al., 2010). On the other hand, it could also indicate that the invasive alien plants took more advantage of the well-watered conditions than the native species did. This would be in line with the idea that invasive plants show higher phenotypic plasticity, and capitalize more strongly on benign conditions than native plants do (i.e. the Master-of-some strategy sensu Richards et al., 2006). In any case, the negative effect of

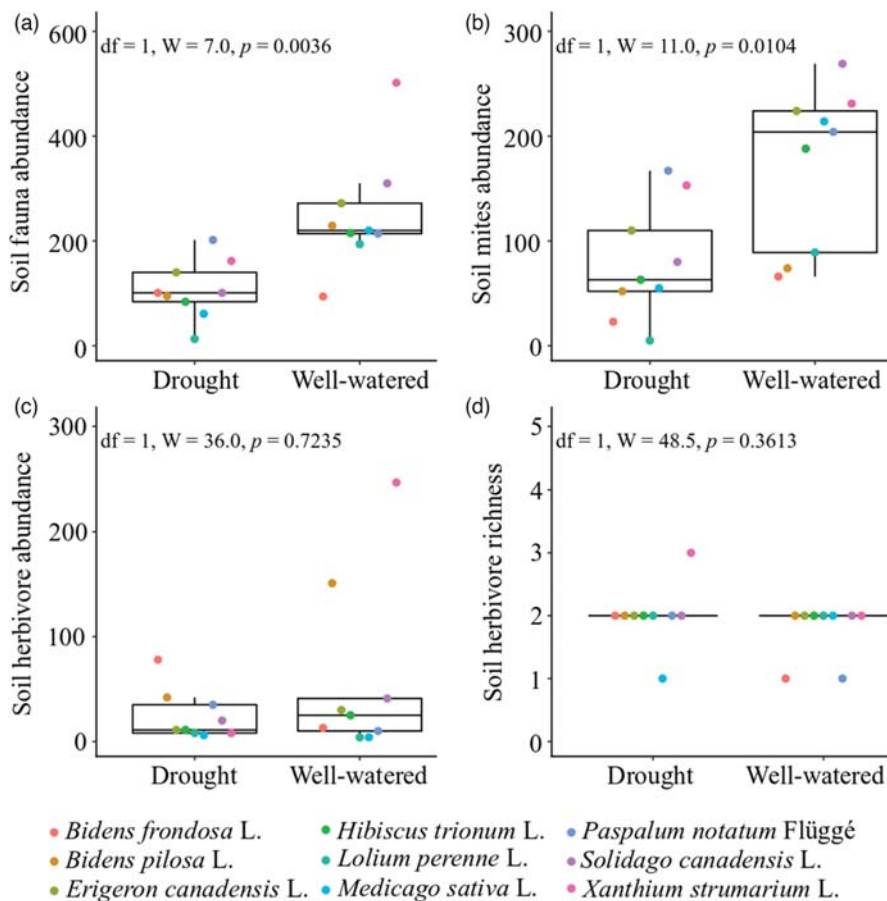


FIGURE 4 Total abundance of soil fauna (a), soil mites (b) and soil herbivores (c), as well as the soil herbivore richness (d) under drought and well-watered conditions. The nine dots of different colours represent samples of the nine pots, each with a different alien target species. Soil herbivores were only identified to the order level and not to the species level.

drought on biomass proportion of the alien plants suggests that the competitive balance between invasive alien plants and native plants could be changed by drought in favour of the resident community. Another recent study, however, showed that alien species that are not invasive yet could benefit more from drought relative to resident plants (Haeuser et al., 2019), which would imply a possible turn-over in invasive alien species with ongoing climate change.

Inoculation with soil fauna significantly increased the biomass production of the native community. It is often suggested that soil mesofauna, such as collembolans and mites in our study (Table S2), could enhance soil-nutrient mineralization and consequently nutrient absorption of plants (Bardgett & Chan, 1999; Lussenhop & Bassirrad, 2005). As a consequence, soil mesofauna frequently has positive effects on plant performance (Lussenhop & Bassirrad, 2005; Mehring & Levin, 2015; Partsch et al., 2006). However, we found that soil-mesofauna inoculation had no statistically significant effect on growth of the alien target plants. Therefore, it is unlikely that soil mesofauna promoted native plant growth by increasing nutrient availability, as we would have expected the invasive alien species to benefit too from additional nutrients. To confirm this, we further measured the total nitrogen and alkaline hydrolysable nitrogen (i.e. *plant-available* nitrogen) of 36 soil samples (20% of total pots) from the drought treatment. This showed that soil-mesofauna inoculation did not significantly affect both types of soil nitrogen (Figure S5).

Another possible explanation for why soil-mesofauna inoculation significantly increased biomass production of the native community

is that the soil herbivores shifted the competitive balance between the invasive alien and native species. This is because invasive alien species—in contrast to native plant species—are often assumed to be largely naïve to the generalist herbivorous soil fauna in their new ranges (Parker et al., 2006; Verhoeven et al., 2009), although they may have been released from their native specialist enemies (Blossey & Notzold, 1995; Chun et al., 2010). However, as in our structural equation model, the correlation between native and alien plant biomass was not significant, this indicates that soil-mesofauna inoculation could only directly increase the biomass of native species rather than indirectly via release from intense competition with aliens. Therefore, our finding that native species produced more above-ground biomass in the presence of soil mesofauna might indicate that compensatory growth in response to herbivory actually resulted in overcompensation (Garcia & Eubanks, 2019; Ramula et al., 2019). Indeed, it has been previously shown that collembolan, at intermediate densities, could enhance plant growth through herbivory-induced overcompensation (Gange, 2000). Although this could explain why the soil fauna suppressed the dominance (i.e. biomass proportion) of alien target plants, future experiments that explicitly test such soil-herbivory-induced overcompensation are needed. Nevertheless, although it has been shown before that soil fauna affects the composition of plant communities (Eisenhauer et al., 2010; Wardle et al., 2004), this is one of the first studies to document the ability of the soil fauna to provide resistance against alien plant invasion.

Although numerous studies have shown that climate change could affect the interactions of plants with above-ground organisms at other trophic levels (de Sassi & Tylanakis, 2012; Eisenhauer et al., 2012; Meza-Lopez & Siemann, 2020; Nooten & Hughes, 2014), only few studies have addressed how climate change may affect interactions of plants with below-ground organisms at other trophic levels (Classen et al., 2015; Eisenhauer et al., 2012; Guyer et al., 2018; Wilschut & van Kleunen, 2021). To the best of our knowledge, no study has addressed how climate change interacts with resident soil fauna to affect competition between native and invasive plant species. Many previous studies found that drought could decrease the abundance of soil fauna (Aupic-Samain et al., 2021; Eisenhauer et al., 2012; Kardol et al., 2010; Lindberg, 2003; Makkonen et al., 2011). Our study provides further support for this, but also shows that drought mainly decreased the abundance of soil mites rather than soil herbivores. Given that drought also decreased the growth of native plants, the persistent soil-herbivore abundance should have resulted in a higher damage intensity. To compensate for this, the native plants, due to their long co-evolution history with the soil herbivores, most likely re-allocated more biomass from above-ground to below-ground structures under drought (Karban, 2011). Although this could not be tested in the present study, this could explain why the growth promotion of native plants induced by soil fauna was stronger under well-watered conditions than under drought.

Interestingly, we found tentative evidence that the decrease in dominance of alien target plants caused by drought was larger in the absence of soil fauna than in its presence. In other words, the presence of soil fauna might buffer against the negative effects of drought on alien plant invasion in resident communities. This is because soil fauna did not mediate the drought effects on the growth of alien plants, which were most likely released from their native enemies. On the other hand, it amplified the negative effect of drought on the growth of native plants. Although our study was only a short-term experiment (8 weeks), the short-term benefit of soil fauna for invasive alien species in response to drought may result in a priority effect (Fukami, 2015; Weidlich et al., 2018), resulting in a long-term advantage for invasive species. However, as such buffering effects of soil fauna for plant invasion under drought may vary across different life stages, more comprehensive tests are required that consider all life stages (e.g. from germination to reproduction). Nevertheless, our study indicates that previous pot experiments that did not consider interactions between soil fauna and plants might have overestimated the effects of drought on alien plant invasion. Therefore, future studies testing the effects of climate change on alien plant invasion should also consider the role of below-ground trophic interactions.

#### 4.1 | Study limitations

Although our study shows that soil-mesofauna inoculation may mediate the drought effects on alien plant invasion in a native

community, our study has several caveats that should be addressed in future studies. First, the approach we used to extract and inoculate soil mesofauna cannot fully exclude side effects of soil micro-organisms that might have been co-inoculated, on competition between the alien and native plants. Given that soil micro-organisms may be pathogenic or mutualistic, and thus may affect plant invasion differently, future studies should explicitly test their specific roles in mediating alien plant invasion under climate change. Second, although plant wilting is frequently used as an indicator of drought stress (e.g. Engelbrecht et al., 2007; Li et al., 2018), it resulted in large variation in the number of days between water-supply points in our drought treatment (range = 1–18 days). As this variation could have affected the soil mesofauna, and thus proportional alien biomass, we recommend that future studies use direct soil-moisture measurements instead of plant wilting. Third, we found that not all alien target species showed similar responses to the drought and soil-mesofauna inoculation treatments. To investigate whether such variation among alien species is caused by, for example, differences in growth form or continent of origin, future studies should include more species and more replicates per species.

## 5 | CONCLUSIONS

The findings of our multi-species experiment are in line with results of previous studies that drought can inhibit alien plant invasion into native resident communities. However, to the best of our knowledge, we here show for the first time that the presence of soil mesofauna might help the resident plant community to resist alien plant invasions. This soil-fauna-mediated resistance may be partly negated by drought. This implies that with ongoing climate change, and more frequent droughts, alien plants might be more likely to overcome the resistance provided by soil fauna.

## AUTHORS' CONTRIBUTIONS

Y.L. conceived the idea and designed the experiment; H.J. and L.C. performed the experiment; H.J. and Y.L. analysed the data; H.J. and Y.L. wrote the first draft of the manuscript, with further inputs from M.v.K. and L.C.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.



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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.